OBSERVATIONS ON THE DEVELOPMENT OF THE MARSUPIAL SKULL.

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(Plates x.-xvii.)

So far as I am aware, almost nothing has been published on the development of the marsupial skull. In 1885, Kitchen Parker published his magnificent monographs on the development of the skull in the Edentata and Insectivora, and he informs us that he had intended to follow these with accounts of the skulls of the marsupials and monotremes; and we know, from various references, that he had done much work on both groups. His death, however, in 1890, interfered with his plans, and no one else has ever taken up the work.

Apart from the references in Parker's papers, almost the only work that seems to have been done on the young marsupial skull consists of various observations that have appeared in papers dealing with other points in the embryology. References to most of these will be found in the list of literature.

The present piece of work was commenced, and most of the sections cut, twelve years ago, but it was found impossible to go on with the research satisfactorily, as so little work had been done on the very early stages of other groups of the higher vertebrates. While Parker's work exhaustively treats of the later development, his methods were not suited to the study of the earliest stages. Our knowledge of the early development of the skull of even the commonest mammals is still very imperfect, and it is difficult to say whether some of the features of the marsupial development are peculiar to the group or may be common to other mammals. So far I have been able to examine and compare the early chondrocrania in *Homo, Ovis, Sus, Talpa.*

Procavia, *Gallus*, *Struthio*, *Chameleo*, *Agama*, *Scapteira*, *Eremias*, *Zonurus*, *Sphenodon* and *Testudo* among the higher vertebrates, but one or two points in the marsupial structure still remain obscure. I think it advisable, however, at this stage to publish an account of the facts of development, leaving to some later date the clearing up, if possible, of those points whose interpretation is doubtful.

The marsupial which I have chiefly studied is the diprotodont, *Trichosurus vulpecula*, of which I have a very complete series. A short account of the external and, to some extent, of the internal characters of the embryos, with figures of the more important specimens, was published some years ago by this Society. Through the kindness of my friends, Professors J. T. Wilson and J. P. Hill, I am enabled to give an account of an interesting early stage of the polyprotodont *Dasyurus viverrinus*.

TRICHOSURUS VULPECULA. Stage i.

Four embryos which may be regarded as belonging to this stage have been cut and examined. These are the embryos referred to in the above-mentioned paper as A, B, C, and E; and they vary in length from 8·5 mm. to 11 mm. In embryo A, only the back part of the head has been preserved, but the degree of chondrification does not differ greatly from that of B and C. In these latter two the cranium is well preserved, and shows very satisfactorily the early condition. The embryos are about the same size, and there are only a few points of difference in the degrees of development. Embryo E is a little in advance of the other, but not greatly. The following description of the condition of Stage i., is taken from embryo C, unless otherwise stated.

The skull at this stage is particularly interesting and, in one or two respects, unlike what was expected from Parker's work on the pig. The cranial axis is fairly well chondrified. In the occipital region it is present as a broad, curved sheet in which there are two foramina, both apparently for branches of nerve xii. A little in front of this region the basal cartilage becomes much narrowed to accommodate the auditory capsules. Between the posterior end of the capsule and the occipital cartilage is a large foramen for the passage of nerves ix., x., and xi. The auditory capsule is well developed, but chondrification has only just begun, and most of the capsule is still in the procartilage stage. It extends far up by the side of the brain, and merges in the ill-defined band of procartilage which supports the lateral wall of the brain. At the plane of the front of the auditory capsule the basal cartilage is much narrowed, but on passing a little forward it is found to again rapidly widen. The notochord ends near the point where the expansion begins. The expanded portion is about double the width of the constricted, and, towards the outer part of the expansion, there is a large oval foramen for the carotid artery. Along the outer part of the expanded part and a little distance from it, lies an elongated, oval bar of cartilage unconnected with any other, and which, as it ultimately develops into the alisphenoid bone, may be called the *alisphenoid cartilage.* A little in front of the plane of the carotid foramen, the basal cartilage becomes again narrowed, and, in the middle line, there is an oval foramen of about the same size as that for the carotid artery, which represents the pituitary fossa. In front of the fossa, for a considerable distance, the basal cartilage is very manifestly seen to be composed of two trabeculæ conjoined in the middle line. In the posterior nasal region the double origin of the cartilage becomes less marked, and from here forward, to near the front of the snout, there is little or no evidence of a double origin. Whether the whole of the nasal septum is trabecular in origin is doubtful, but the base, at least, is pretty manifestly the anterior continuation of the trabeculæ. The nasal capsule is very imperfectly chondrified, but the arrangement can be made out fairly easily. It may be described as a cylindrical structure with three openings, one at the anterior end looking outwards, the anterior nasal opening; a second opening downwards into the mouth, the internal nares ; and a third opening upwards and backwards, the opening for the nerves. The inferior opening is bounded on the inner side by a strip of cartilage or procartilage which runs along parallel to the base of the nasal septum. This is the structure which has been called by Parker the "recurrent cartilage," and by others the "paraseptal cartilage." As I think there is good reason for believing that Parker's view of its being trabecular in origin is erroneous, the latter term seems preferable.

Meckel's cartilage is pretty well chondrified and of large size. Posteriorly it passes into the badly defined condensation of cells which represents the auditory ossicles. The hyoid is a small, cartilaginous, curved rod which passes inwards to meet the median basihyal. A well defined thyroid can likewise be readily made out, also meeting the basihyal.

The relationships of many of the structures will be better understood from the actual sections than from the reconstruction; and I have, therefore, given figures of a number of the more important with brief descriptions.

Section A (Plate x., fig. 2). This section is through the anterior nares, and shows the nasal capsule imperfectly chondrified. The two capsules unite at the median septum, but whether the septum is really part of the capsule or an anterior development of the trabeculæ, is not apparent from the section. There is some reason to believe that the lower part, at least, of the septum is trabecular.

Section B (fig. 3). This is a transverse section near the middle of the nasal capsule, and through the front of the opening between the nose and the mouth. As yet the secondary palate, though in large part formed, is widely open, and the tongue lies between the two halves of it. The alinasal cartilage is well developed and slightly chondrified, as is also the septum. By the side of the base of the septum the paraseptals are distinctly seen, but imperfectly chondrified. Below the lower part of the alinasals are seen the large groups of osteoblasts about to form the maxillæ. At this plane is seen also the anterior union of Meckel's cartilages (not shown in the figure).

Section C (fig. 4) is only a short distance behind B, and is figured to show Jacobson's organ. The organ is unusually short, being seen only in eleven sections, and opens directly into the nasal cavity.

Section D(fig.5) is near the posterior end of the nasal capsule, and shows the paraseptal still of large size. The septum is only well differentiated at its base, which is clearly trabecular. The upper part is unchondrified, and may perhaps belong to the capsule. A portion of the alinasal is seen to the outer side of the nasal cavity. The section is through the anterior end of the cranial cavity and some of the branches of the olfactory nerve.

Section E (Pl.xi., fig.6) is through the pituitary opening and the anterior part of the alisphenoid cartilage. The trabeculæ are oval on section, and separated from each other. Between them the stalk of the pituitary body is seen, and above them the anterior part of the hypophysis. At some little distance outside of the trabecula and a little below the level of it, is seen the large, round, alisphenoid cartilage. It lies in the base of the palatal ridge. Outside of it and above it lies the maxillary branch of nerve v. The orbitosphenoid band, though not chondrified, can be distinctly seen.

Section F(fig.7) is through the posterior part of the alisphenoid cartilage, and shows the basal cartilage perforated for the carotid artery. Only a very small bar of cartilage lies outside of the artery. A little further out is the still rounded alisphenoid cartilage. Directly above it lies the very large Gasserian ganglion, while above the ganglion can be seen the orbitosphenoid band. The hyoid and the thyrohyal cartilages are both seen articulating with the basihyal, and below the thyrohyal the thyroid cartilage is so situated as to suggest that it is serially homologous with the hyoid and thyrohyal, and represents the second branchial arch. (They are omitted from the figure).

Sections G and H are from embryo B, as the head of this embryo has been cut so that the sections of the posterior half are more directly transverse than in embryo C.

Section G(fig.8) is through the anterior part of the auditory capsule. The basal cartilage is flat and narrow. The capsule is of large size, but not very distinctly chondrified. At the lower part the uncoiled cochlea is seen in section. Above it is a portion of the cochlear ganglion of nerve viii.; and to the outer side of this latter lies nerve vii., with its geniculate ganglion. Meckel's cartilage is at this point imperfectly chondrified.

Section H(fig.9) is through the posterior part of the capsule. Here the basal cartilage is broadening out but is still flat. The capsule is of large size, and in its upper part is seen the expanded labyrinth with, on the outer and upper sides, portions of the semicircular canals, and, at the upper and inner part, the base of the recessus labyrinthi.

TRICHOSURUS VULPECULA. Stage ii.

This stage represents the degree of development attained by the Phalanger at birth, when the embryo measures 14 mm. in greatest length. The skull is now well chondrified, and the bones of the jaws are ossified. In general structure it is as simple as in the earlier stage, but a number of the elements can now be made out with greater clearness, while some previously distinct are now fused with others.

The nasal capsule is still a simple, elongated, cartilaginous cylinder with three openings in it—an anterior external for the anterior nostril, a posterior superior for the olfactory nerves, and an inferior opening for the internal nasal opening. The nostril opens directly outwards, and is completely surrounded by cartilage above, in front, and behind. Inferiorly the nostril is imperfectly floored by a cartilaginous flap which passes forward from the base of the alinasal. There is no fenestra in the septum. The paraseptal cartilage is still complete, and runs by the side of the base of the nasal septum to the back of the nasal cavity, where it is joined by a broad bar to the base of the alinasal.

The upper and outer part of the alinasal is continued backwards as a broad cartilaginous bar lying by the side of the brain, and forming a support to it, and joins the upper part of the auditory capsule. This is the orbitosphenoid cartilage. In front, besides joining the alinasal, it also joins the basal cartilage, and a small fenestra is formed between its two attachments.

The basal cartilage, on passing back from the nasal region, broadens out gradually, and, on reaching the plane of the pituitary opening, it is found to form a very broad plate by having become united to the alisphenoid cartilage. The alisphenoid cartilage differs from that of the earlier stage in there being now seen an upward growth from near the middle of the outer side. This ascending process lies between the second and third branches of nerve v., and the Gasserian ganglion itself rests, as in the earlier stage, on the alisphenoid cartilage. The carotid foramen is still of large size, and is completely surrounded by cartilage.

The auditory capsule is large and fairly well chondrified. The lower part is oval, and the chondrification is less perfect. This part lodges the small cochlea, as yet uncoiled, and the greater part of the saccule and utricle. The upper part of the capsule is well chondrified, and is structurally continuous with the orbitosphenoid bar. It protects the upper part of the utricle and the semicircular canals. The fenestra ovalis is situated a little below the middle of the capsule. From the upper part of the capsule there is given off a cartilaginous ridge which passes downwards and protects the tympanum. This is the tegmen tympani. It is not quite clear whether it is a part of the auditory capsule or a process from the exoccipital.

Behind the lower part of the capsule there is an elongated fenestra for the passage of nerves ix., x., and xi. The occipital cartilage behind this is broad and well developed. There are two foramina, both apparently for nerve xii. There is no apparent differentiation between the basioccipital and the exoccipital, but the supraoccipital can be demarcated from the exoccipital.

Meckel's cartilage is well chondrified, and is continuous with the anterior process of the malleus. The malleus is fairly large, but the capitulum is not very marked, and the manubrium rather short and directed markedly inwards. The incus articulates with the malleus in the usual manner, and is of the usual mammalian shape. The stapes is large and is perforated.

The hyoid articulates in part with the processus longus of the incus, and in part with the margin of the tegmen tympani.

The premaxillary bone is partly ossified. It forms a support for the germs of the incisor teeth, and a floor for the anterior part of the nasal capsule. In the cleft between the nasal capsules in front there are indications of an ascending internasal process, as in reptiles. The process is not ossified, but the strand of differentiated cells, perhaps degenerate osteoblasts, can be easily traced into the region to be occupied by the nasal bone.

The maxilla is a triangular-shaped bone when viewed from below. It is most developed in the region of the teeth-germs, but the secondary palate is well formed. The roof of the mouth is markedly concave.

The palatine is well ossified and forms the walls of the posterior nares. The portion which forms the secondary palate is the larger.

The pterygoid is still small, and only partly ossified. It rests on the lower part of the anterior end of the alisphenoid cartilage.

The jugal, the lachrymal, and the squamosal are beginning to ossify, but too imperfectly to be drawn.

The mandible is well ossified and of large size. At its posterior end the coronoid process and the angle are already typically formed, and the articular condyle is made up of cells somewhat like imperfectly formed cartilage-cells, but there is no distinct cartilage.

The following series of sections will illustrate the relationships of the more important structures. Section A is from the unborn embryo described and figured as embryo F. All the other sections are from the newly born embryo described and figured as embryo H.

Section A (Pl. xiii., fig. 13). This section has been figured from the unborn specimen as, owing to the different staining, the cells of the developing premaxilla are better seen. The section is through the front part of the anterior nares. Part of the capsule is seen as a half ring, which is a short distance apart from that of the opposite side. Between the two cartilages are seen the strands of cells which represent the ascending internasal processes of the premaxillæ.

Section B (fig.14) is through near the middle of the external nares. The nasal capsules are seen joined in the middle line. A portion of the premaxilla is seen below the base of the cartilage. The flap of cartilage, which passes forwards and forms a floor to the nostril, is cut across. In the lower jaw (not figured) the symphysis of Meckel's cartilages is seen, and a portion of the dentary.

Section C(fig.15) is through the posterior border of the nostril. The nasal septum now shows no sign of having a double origin. Inferiorly it passes far down towards the papilla palatina, and is wedged between the premaxillary bones. The cartilage of the nasal floor extends inwards to the base of the septum, against which it abuts. Above its outer end is a small triangular piece of cartilage which stretches across from the alinasal at the back of the nasal opening, to the nasal floor-cartilage. The front of the maxilla is cut across.

Section D(fig.16) is through the posterior part of the nasal capsule. The alinasal cartilage is open above; and, attached to its upper part, is the large orbitosphenoid cartilage. The lower part is short and thick. The paraseptal is seen joining on to the middle region of the alinasal. The median or septal cartilage is short and broad. The maxilla appears to be much thickened, but this is due to the secondary palate being cut obliquely. The lachrymal can be detected, but it is not yet ossified.

Section E (Pl.xiv., fig.17) shows the relations of parts at the anterior end of the alisphenoid. The basal cartilage is partly divided by the almost obliterated pituitary canal. External to it lies the rounded alisphenoid. Above the alisphenoid is seen the second branch of nerve v., and further up the well developed orbito-sphenoid cartilage.

Section F(fig.18) is through the middle of the alisphenoid cartilage. At this stage the cartilage differs from that of the earlier in having an upward growth towards the orbitosphenoid on the outside of the Gasserian ganglion. Though the alisphenoid is partly fused with the basal cartilage, the division is still well marked. Meckel's cartilage is of large size, and has the dentary lying on its outer side.

Section G(fig.19) shows the relation of parts at the posterior end of the alisphenoid. The basal cartilage is perforated by the carotid artery, and the alisphenoid lies partly below the outer portion. The Gasserian ganglion is here of large size, and fills in the whole space between the basal cartilage, the alisphenoid, and the orbitosphenoid.

Section H(fig.20) is through the anterior part of the auditory capsule. The basal cartilage is a broad, fairly thick, flat plate. To its outer side is attached the auditory capsule, which here contains the cochlea. The anterior end of the cochlea is curved outwards, and the section is across the curved portion. There is no coiling as yet, the curve forming less than a semicircle. Resting on the outer side of the auditory capsule is the geniculate ganglion of nerve vii. A little outside of the ganglion is the malleus cut in section. Below the malleus and the auditory capsule is seen the Eustachian canal and tympanic cavity, and a little external to this is the external auditory meatus filled with epithelium. The orbitosphenoid is much smaller than in the anterior sections. Inferiorly both the hyoid and the thyrohyal cartilages are seen in section.

Section I(Pl.xv., fig.21) is through the middle of the auditory capsule. The section does not differ very greatly from the preceding The upper part of the capsule is now seen united with the posterior part of the orbitosphenoid bar. The utricle, saccule, and posterior end of the cochlea are seen in section. Portions of the incus and stapes are shown, and internally much of nerve viii., is seen.

Section J(fig.22) is considerably further back than Section I. The utricle and the ductus endolymphaticus are seen lying side by side inside the upper part of the cartilaginous auditory capsule. Two semicircular canals are seen in section. The lower part of the auditory capsule has almost disappeared. The basal cartilage is now much broader; and, in the space between it and the auditory capsule, is seen the ganglion of nerve x. On the outside of the capsule is seen the tegmen tympani, which, in this section, is differentiated from the capsule. Above, the capsule is continued into a slender bar of cartilage, from which it is somewhat differentiated. When the whole series of sections is traced, this cartilage is seen to be continuous with the supraoccipital behind, and in front it becomes merged in the cartilage which may be either the upper part of the auditory capsule, or the posterior part of the orbitosphenoid.

Section K(fig.23) is through the posterior part of the capsule. The section is interesting as showing that the capsule is here very distinct from the supraoccipital above, and from the basal cartilage below. To the inner side of the capsule lies the ductus endolymphaticus. In the lower part of the large basal cartilage is seen the posterior of the two foramina for nerve xii.

Section L(fig.24) is a little behind the previous one, and shows the supraoccipital, now of large size and united with the outer part of the basal cartilage, which may be regarded as the exoccipital. On the inside of the supraoccipital lies the large saccus endolymphaticus.

DASYURUS VIVERRINUS. Stage ii.

The earliest stage of the Native Cat which I have been able to study, is a mammary fœtus probably but a few days old. The head measures 4 mm., and the greatest length in the curved position 8 mm. Though much smaller than *Trichosurus* at birth, it is quite as well developed, the cartilages being well chondrified and many of the cranial bones ossified. Though the skulls of the two types of marsupials are in the main essentially similar, the differences are very much greater than one would be inclined to expect.

The general structure of the chondrocranium will be most readily understood by examining figures 25 and 26 (Plate xiv.) and comparing them with those of the early cartilaginous skulls of *Trichosurus*. Relatively in *Dasyurus* the nasal portion of the skull is much larger, the orbitosphenoid much broader, and the inferior part of the auditory capsule much smaller than in *Trichosurus*. But besides these differences in degree of development there are a number of points of difference of a more fundamental nature.

The nasal capsule has the anterior nares relatively further forward than in *Trichosurus*, so that, whereas in the latter the premaxilla lies underneath the middle of the opening, in *Dasyurus* the whole of the opening is in front of the bone. There is a further difference in that while *Trichosurus* has a very imperfect cartilaginous floor, in *Dasyurus* the floor is well developed. The paraseptal cartilages are large in front, and pass backwards to near the end of the nasal capsule; but posteriorly they do not fuse with the back part of the capsule as in *Trichosurus*. Posteriorly the nasal cartilages fuse with the median cartilage and form a broad, flat, cranial floor.

At this stage the alisphenoids are, as in the second stage of *Trichosurus*, fused to the cranial floor-cartilage. They are, however, clearly differentiated from the median cartilage. From the anterior and outer corner there passes upwards, outwards, and forwards, a slender cartilaginous process which, at its upper end, joins with the orbitosphenoid cartilage. Though in a number of respects unlike the ascending process seen in *Trichosurus*, it is doubtless homologous with it, as in each case the cartilage lies between the second and third branches of nerve v. The carotid foramen is relatively smaller in *Dasyurus*.

The orbitosphenoid cartilage is very large, and is completely fused with the nasal capsule in front and the auditory capsule behind. Less distinctly it is continued into the supraoccipital.

Owing to the imperfectly developed state of the cochlea at this stage, the lower part of the auditory capsule is small, but the upper part containing the semicircular canals is quite as large as in *Trichosurus*.

The occipital region is relatively short. There are two foramina for nerve xii., and a large opening is left in front for nerves ix., x., and xi. The occipital cartilage meets the auditory, but does not fuse with it, except above the level of the semicircular canal.

The premaxillary maxilla, palatine, pterygoid, jugal, and the mandible are all ossified at this stage. The premaxilla is small, and situated far behind the anterior part of the nasal cartilage. The maxilla is flat, but has two well marked ridges bounding the dental region. The secondary palate is but imperfectly developed. The palatine is large, and forms a good secondary palate. The pterygoid is very small, and, as in *Trichosurus*, develops in connection with the alisphenoid cartilage.

The malleus, incus, and stapes are shown in fig.26*a*(Plate xvi.). The manubrium of the malleus is not fully chondrified. The incus is not unlike that of the higher mammals. The elements are relatively large.

In Plate xvii., are shown six typical sections through the head of the young *Dasyurus*. The head was cut into 305 sections, and the number of the section will indicate the plane.

Section A(fig.47) is the 44th of the series. It passes through the external nasal opening, and shows the condition of the nasal cartilages. The great development of epithelium inside and outside of the mouth, with the fusing of the lips, are well seen.

Section B(fig.28) is the 75th, and in a plane immediately behind the nasopalatine canal. It shows the nasal septum no longer attached to the alinasal, while the upper part of this latter is passing into the large, lateral orbitosphenoid cartilage. Below the organs of Jacobson lie the paraseptals. The maxillary bone is seen in section with a small secondary palatal plate. Below the tongue is seen the developing mandible, which is ossified considerably in advance of Meckel's cartilage, appearing in the 60th section, while the cartilage only appears at the 85th.

Section C(fig.29) is the 122nd, and passes through the middle of the eye. The median cartilage is here broadened out, and fused with the back part of the alinasal. The orbitosphenoid is large, aad appears fused to the median cartilage. The upper two-thirds are well chondrified, but the lower third partly fibrous Portions of the maxilla are seen, and the small jugal is cut across. In the lower jaw Meckel's cartilage is shown, with the mandibular ossification lying on and above it.

Section D(fig.30) is Section No.173. The median cartilage is broad, and is pierced by the foramen for the carotid. The alisphenoid cartilage is small, and closely united to the basal cartilage. On its inner and under side lies the ossifying pterygoid. Meckel's cartilage is seen cut obliquely as it passes up to unite with the malleus. The mandible is still seen in close connection with it. The orbitosphenoid is now far removed from the lower cartilages, and forms a protecting shield for the side of the brain.

Section E(fig.31) represents Section No.204. It cuts the anterior part of the auditory capsule, the lower part of which is seen supporting the cochlea. Above the cochlea is the ganglion of nerve vii. The upper part of the auditory capsule is seen united to the posterior continuation of the orbitosphenoid cartilage. Both malleus and incus are cut across in the section, and the tympanic cavity, the Eustachian tube, and the external auditory passage are seen.

Section F(fig.32), representing Section No.225, is through near the middle of the auditory capsule. The cochlea, with its nerve and ganglion, is well seen, also one of the semicircular canals. The upper part of the auditory capsule is, as in the previous section, united with the continuation of the orbitosphenoid, and this can be traced right over the brain to join that of the other side. The hyoid and thyroid cartilages are cut across.

Comparison of the Marsupial Primordial Skull with that of the Monotreme.

Since the greater part of this paper has been prepared, and on the eve of its being sent off, I have fortunately been enabled to consult Gaupp's magnificent paper on the early skull of Echidna, which has just appeared this year. It is probably better to leave the main part of my paper exactly as it stands, as most of the conclusions have been arrived at quite independently of any previous work by others. Had I previously seen Gaupp's paper, I should quite probably have adopted one or two of his terms in preference to those used here, and for certain structures to which

I have given no name; but, on the whole, my paper would have remained much as it is. Whether morphologists accept all Gaupp's conclusions or not, all must be most grateful for a most beautiful piece of conscientious work.

When one compares the skull of the very young *Echidna* with that of the young *Dasyurus*, one is at once struck by the remarkable similarity between the two. In fact the Dasyure skull resembles that of *Echidna* more than it does that of *Trichosurus*.

Echidna agrees with *Dasyurus* in having a broad, flat, nasal floor-cartilage (*solum nasi*), and in having the paraseptal cartilages ending in a point. There is an absence in *Dasyurus* of the palatine-process of the solum nasi, seen in *Echidna*. The nasal capsule behind joins the median cartilage in much the same way in both.

The cartilage which I have called the alisphenoid, Gaupp calls the *ala temporalis*. It is similarly situated in the Dasyure and *Echidna*, but the marsupials reveal the meaning of the structure much better than the monotreme. In *Echidna* there is a small cartilaginous process passing upwards and forwards to join the orbitosphenoid, but this is apparently not homologous with the process in *Dasyurus*. The position of the carotid foramina differs somewhat, being much nearer the middle line in *Echidna*. The marsupial condition is thus intermediate between the monotreme and the eutherian.

The parachordal region in *Echidna* is a little narrower than in *Trichosurus*, and much narrower than in *Dasyurus*. The occipital cartilage differs in having, in the marsupials, two foramina for nerve xii.; while, in *Echidna*, nerve xii. passes, according to Gaupp, with x. and xi., through the jugular foramen.

The auditory capsules resemble each other in the two groups owing to the cochlea being simply curved and not coiled in either. The section shown by Gaupp in Plate lxxii., fig.19, should be compared with my fig.31, and the near affinity of the monotreme and the marsupial will be manifest. In all essential features there is close agreement.

The large lateral cartilage which I have referred to as the orbitosphenoid, Gaupp calls by various names. The anterior part he calls the *ala orbitalis.* A little further back it is called the *commissura orbito-parietalis;* while, when it passes above the auditory capsule, it becomes the *lamina supracapsularis.* In *Echidna*, however, the cartilage is essentially similar to that in the marsupials.

The monotreme auditory "ossicles" chiefly differ in the small size of the incus.

Comparison of the Marsupial Primordial Skull with that of the Eutheria.

Much more work requires to be done before anything like a satisfactory comparison can be made, and the Eutherian orders appear to differ about as much from one another as the marsupial does from them. As soon as I can obtain some leisure from more pressing other work, I hope to give reconstructions of the very early skulls of a number of types.

In the eutherians the most noticeable character is the large size of the cochlea which, even before chondrification, is coiled, so that the lower part of the capsule is always large. The orbitosphenoid cartilage extends the whole way from the nasal to the auditory capsules, but is usually smaller than in the marsupials; and the optic nerve passes through it. The paraseptal cartilage never, so far as known, unites with the capsule behind, as in the Diprotodonts. The alisphenoid cartilage is always apparently present, as in marsupials; and is, as in marsupials, quite a distinct cartilage originally. There is good reason to believe that it is this cartilage that Parker, in his work on the pig's skull, took for the palatopterygoid. The carotids in the higher mammals do not pierce the basal cartilage, and nerve xii. has only a single foramen.

The Fundamental Structure of the Mammalian Skull.

The study of the early development of the marsupial and eutherian skulls leads one to differ considerably from the conclusions of Parker as to the fundamental structure of the skull. The vertebrate skull is usually regarded as made up of the following elements—a pair of parachordals, a pair of trabeculæ, a pair of nasal capsules, a pair of ear-capsules, and a series of visceral arches, with secondary developments of these. By many, the occipital elements are looked upon as a cranial vertebra and distinct from the parachordals. It might seem unlikely that the development of the skull of the mammalia—the highest group of the vertebrates—should reveal the fundamental structure more clearly than that of the lower groups; but, as regards the skull, the mammal is much simpler than the reptile, and less degenerate than the living amphibians. In *Trichosurus* the elements are more easily differentiated than in *Dasyurus*, presumably because the embryo is considerably larger when chondrification begins; and, in some of the Eutheria, points can be made out which are obscure in the marsupials.

The parachordals and trabeculæ are very definite structures, but the occipital region is not very clearly differentiated from the parachordal. The trabeculæ form all the median, basal cartilage in front of the parachordals. There is good reason to believe, however, that the paraseptals are not recurrent trabecular cornua, as supposed by Parker, but true parts of the nasal capsule, and probably only the base of the nasal septum is trabecular, the upper portion being part of the nasal capsule. The large lateral cartilage, which I have spoken of as the orbitosphenoid, seems to be as definitely a cranial element as the trabecula. It passes from the nasal capsule backwards, forming a lateral wall to the brain; and, while in *Echidna* and the marsupials it fuses with the auditory capsule, forming the *lamina supracapsularis* of Gaupp, it is manifest from some of the eutherian embryos that it is quite a distinct element from the auditory capsule, only uniting with it late. There is also some reason to consider that the supraoccipital is the further continuation of the same band.

The alisphenoid cartilage (*ala temporalis* of Gaupp) in the marsupials and eutherians first appears as a distinct cartilaginous rod which lies below the Gasserian ganglion. It afterwards unites with the outer edge of the trabecula. Still later, a process grows up between the maxillary and mandibular branches of nerve v., and gradually it ossifies into the alisphenoid bone. There is thus no doubt as to its later history: the difficulty is to be certain of its homologies in lower vertebrates. It is undoubtedly not trabecular, and, among reptiles, the only cartilage with which it seems comparable is the palatopterygoid. At first sight this may seem a startling conclusion, but there is much to be said in its favour. In *Sphenodon*, the most primitive reptile which we can examine, and the one nearest to the mammal-like reptiles from which the mammals sprang, we find a bar of cartilage bearing the same relations to the trabecula as the alisphenoid cartilage does in the marsupial. This is the horizontal portion of the palatopterygoid arch. The resemblance is obscured by the development of the upward-passing epipterygoid. When, however, the epipterygoid is aborted, as in *Chameleo*, we get a short cartilaginous bar almost exactly similar. In the snakes the same cartilage gives rise to the so-called alisphenoid bone. In the Crocodilia we again get an alisphenoid bone; and in the Chelonia a small bone which some regard as alisphenoid, others as an epipterygoid. Even among extinct reptiles we get either an alisphenoid or an epipterygoid, but never both. In the Therocephalia and Anomodontia there is a typical epipterygoid; in the Cynodontia a fan-shaped bone takes its place, and in the mammal this becomes the bone we call the alisphenoid.

We may thus conclude that the element which develops into the alisphenoid is a specialisation of a rudiment of the palatopterygoid arch.

LITERATURE.

In Gaupp's paper is given a list of the most important papers on the development of the skull of the higher vertebrates.

[Gaupp, E.—" Zur Entwickelungsgeschichte und vergleichenden Morphologie des Schadels von Echidna aculeata var. typica." Semon's Zoologische Forschungsreisen in Australien, &c., iii. Band, 4 Lief., p.782 (1908)].

REFERENCES TO PLATES X.-XVII.

al.n., alinasal—*a.n.*, anterior nares—*a.Pmx.*, trace of the premaxillary extending round the front of the nasal capsule—*a.s*, alisphenoid—*aud.*, auditory capsule—*b.hy.*, basihyal—*car.*, carotid artery—*c.f.*, carotid foramen—*coch.*, cochlea—*conj.*, conjunctiva—*D.*, dentary—*d.e.l.*, ductus endolymphaticus—*d.l.*, dental lamina—*e.a.c.*, external auditory canal—*e o.*, exoccipital—*f.e.*, foramen epiphaniale—*G.g.*, Gasserian ganglion—*hy.*, hyoid—*in.*, incus—*J.o.*, Jacobson's organ—*Ju.*, jugal—*lab.*, labyrinth—*ma.*, malleus—*Mk.*, Meckel's cartilage—*Mx.*, maxilla—*n.s.*, nasal septum—*o.s.*, orbitosphenoid—*Pa.*, palatine—*pit.*, pituitary—*Pmx.*, premaxilla—*p.s.*, paraseptal cartilage—*Pt.*, pterygoid—*s.e.l.*, saccus endolymphaticus—*s.o.*, supraoccipital—*s.p.*, secondary palate—*thy.*, thyro-hyal—*tr.*, trabecula—*t.t.*, tegmen tympani—*tymp.*, tympanic cavity—*ut.*, utricle; v., vii., viii., ix., x., xi., xii., cranial nerves—vii.*g*, ganglion of nerve vii.—viii.*c*, cochlear ganglion of nerve viii.

Plate x.

Fig.1.—Underview of reconstruction of the skull of a 10 mm. intrauterine fœtus of *Trichosurus vulpecula*(× 22). The parts outlined are distinctly chondrified; in those parts which are coloured, but with dotted outlines, chondrification is imperfect; the parts shaded but not coloured are not chondrified.

Figs.2-5.—Sections through the snout of 10 mm. *Trichosurus* embryo(× 30).

Plate xi.

Figs.6-7.—Sections through the alisphenoid region of the head of 10 mm. *Trichosurus* embryo(× 30).

Figs.8-9.—Sections through the ear-region of head of a different specimen of 10 mm. *Trichosurus* embryo. Cut in different direction(×).

Plate xii.

Fig.10.—Under view of reconstruction of skull of 14 mm. mammary fœtus of *Trichosurus vulpecula*(× 30). The membrane bones are removed from the right side; and Meckel's cartilage, the malleus, incus, stapes and hyoid from both sides.

Fig.11.—Side view of same(× 30).

Fig.11*a*.—Malleus, incus, and stapes of ditto.

Plate xiii.

Figs.13-16.—Sections through the anterior part of the head of 14 mm. mammary fœtus of *Trichosurus vulpecula*(× 45).

Plate xiv.

Figs.17-20.—Sections through the middle region of the head of 14 mm. mammary fœtus of *Trichosurus vulpecula*(× 30).

Plate xv.

Figs. 21-24.—Sections through the posterior part of the head of 14 mm. mammary fœtus of *Trichosurus vulpecula* (× 30).

Plate xvi.

Fig. 25.—Underview of reconstruction of the skull of 8 mm. mammary fœtus of *Dasyurus viverrinus* (× 40). The membrane bones have been removed from the right side; and Meckel's cartilage, the malleus, incus, stapes, and hyoid from both sides.

Fig. 26.—Side view of same (× 40).

Fig. 26*a*.—Malleus, incus, and stapes of same.

Plate xvii.

Figs. 27-32.—Sections through the skull of 8 mm. mammary fœtus of *Dasyurus viverrinus* (× 30).